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POPULATION STRUCTURE AND SITE CHARACTERISTICS OF THE RARE SHASTA SNOW-WREATH (*NEVIUSIA CLIFTONII*)

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ABSTRACT

The Shasta snow-wreath (*Neviusia cliftonii* Shevock, Ertter & D.W. Taylor; Rosaceae) is a rare shrub, endemic to areas near Shasta Lake in the eastern Klamath Range of northern California, USA. Since discovery in 1992, the number of known populations has increased from 3 to 33. Shasta snow-wreath is a thicket-forming shrub, thought to reproduce primarily vegetatively, where individual stems (ramets) arise from the root system. We provide the first descriptions of demography and site characteristics using data collected in eight populations of Shasta snow-wreath. We established permanently-marked transects and recorded the number of ramets, individual stem heights, and the number of inflorescences in 2011, 2012, and 2013. We also characterized sites by tree canopy, shrub components, fuels, vegetation, and ground cover. Using the number of ramets recorded and the total population area, we estimated the number of ramets in each population ('ramet population size'). Ramet population size ranged from 716 to 18,641 (mean = 5467), and the average maximum stem height ranged from 50 to 159 cm (mean = 104 cm). Larger ramet population size and taller stems were both associated with less tree cover. The two largest ramet population sizes were found at the two highest elevations and most west-facing sites. The average number of inflorescences per stem over three years ranged from 0.08 to 4.91 (mean = 2.76) and showed an increase with elevation. How Shasta snow-wreath will respond to succession or disturbances is unknown, but the negative relationship of ramet population size and canopy cover indicates that fire may have been important for influencing the population size historically. Continued monitoring of the studied populations, and the addition of more populations to the monitoring program, would be useful for detecting demographic changes and for better understanding the factors that govern Shasta snow-wreath.

Key Words: demography, eastern Klamath Range, endemism, *Neviusia cliftonii*, population monitoring, rarity, Rosaceae, Shasta Lake, Shasta snow-wreath.

The Shasta snow-wreath (*Neviusia cliftonii* Shevock, Ertter & D.W. Taylor) is a rare shrub in the Rosaceae with a distribution limited to the vicinity of Shasta Lake in the eastern Klamath Ranges of northern California, USA (Taylor 1993; Lindstrand and Nelson 2006; Lindstrand et al. 2016; Fig. 1). Shasta snow-wreath was first discovered in 1992 along Cedar Creek east of Redding, CA, at the base of an exposed, north-facing limestone outcrop (Shevock et al. 1992; Taylor 1993). Because the first three Shasta snow-wreath populations were all found on limestone rock formations, the species was originally described as a limestone endemic (Lindstrand and Nelson 2005, 2006). However, exploration of the region has revealed that most populations (57%) are found on non-limestone substrates such as shale, mudstone, and greenstone (DeWoody et al. 2012). The only congener of Shasta snow-wreath, *Neviusia alabamensis* A. Gray, also has a highly restricted range and occurs in several disjunct populations in the southeastern United States (Long 1989).

It is possible that Shasta snow-wreath was at one time more widespread and has become progressively more restricted to its current, isolated range (DeVore et al. 2005). Fossil evidence of a closely related plant (*Neviusia dunthornei* DeVore, Moore, Pigg & Wehr) in a Pacific Northwest Eocene flora supports the hypothesis that the former range of the species may have stretched as far as British Columbia (DeVore et al. 2004; DeVore et al. 2005). The persistence of Shasta snow-wreath near Shasta Lake has been attributed to the lack of volcanic deposition, glaciation, and the combination of low elevations and high precipitation levels (Lindstrand and Nelson 2006). The number of known Shasta snow-wreath populations has grown steadily from three in 1992, to 17 in 2004, to 23 in 2012 (Lindstrand and Nelson 2005, 2006; DeWoody et al. 2012), and to 33 as of this writing (CDFW 2016; L. Lindstrand III, North State Resources, Inc. personal communication; Fig. 1). The California Natural Diversity Database (CNDDB) lists 24 "occurrences" of Shasta snow-

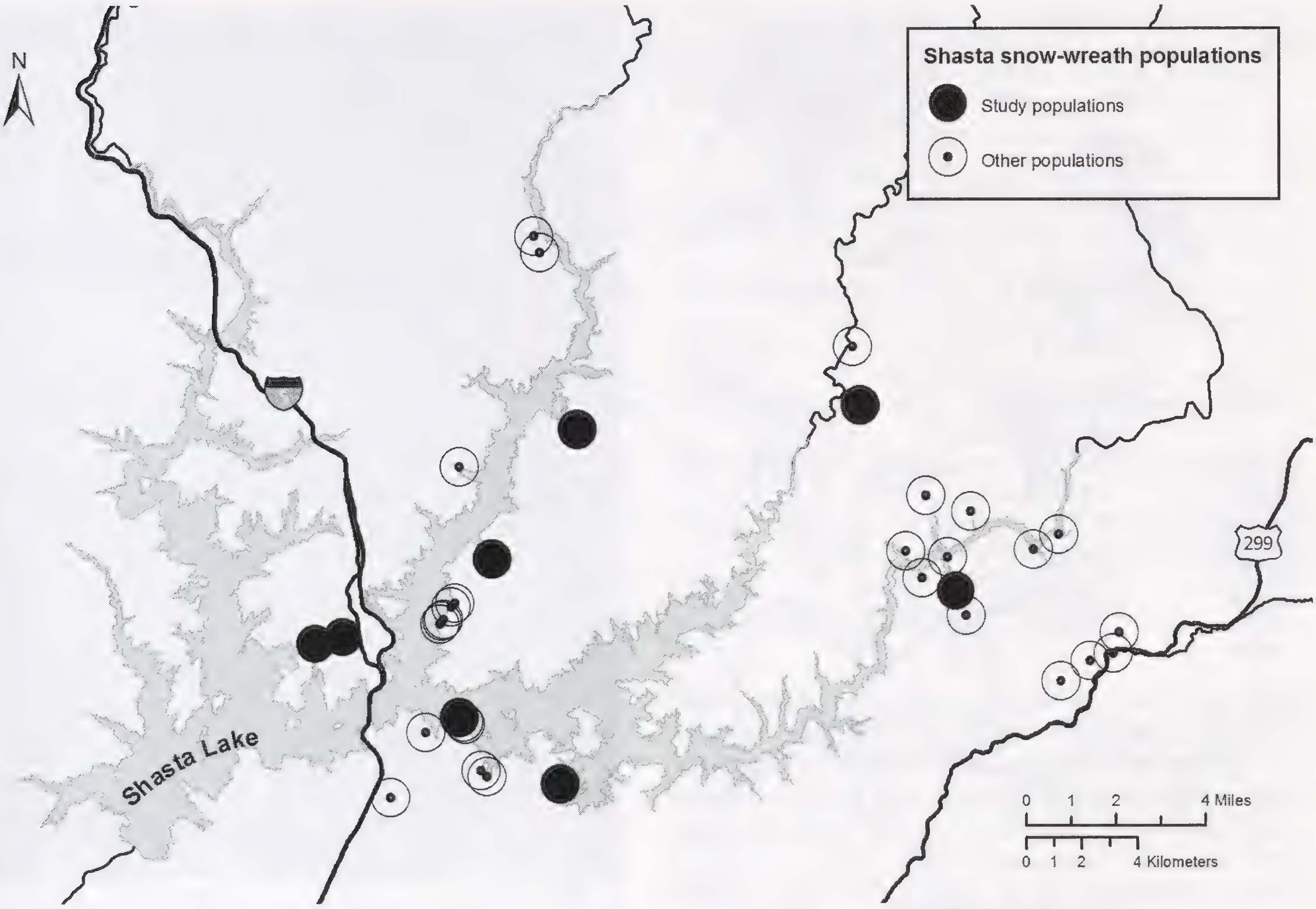

FIG. 1. Locations of all 33 known Shasta snow-wreath populations.

wreath, however an occurrence can include multiple, discrete patches found within 0.25 miles of one another if they are not separated by significant habitat discontinuity (CDFW 2016). In this paper, we term the discrete patches "populations" and use them as our focus of discussion. All of the known populations are found within the Cow Creek, McCloud River, Pit River, Sacramento River, and Squaw Creek watersheds near Shasta Lake, which was formed in 1945 when Shasta Dam was completed. Whether the formation of the lake destroyed some populations of Shasta snow-wreath and further restricted its range is unknown, but seems likely, given that populations are found directly adjacent to the lake. A plan has been proposed by the U.S. Bureau of Reclamation that would raise the height of Shasta Dam up to 5.6 m and flood additional terrestrial habitat (U.S.D.I. 2015). Previous analyses suggest this lake expansion project would submerge portions of nearly 40% the known Shasta snow-wreath populations, though only ~3% of the total habitat occupied by the species would be submerged (U.S.D.I. 2014). Nonetheless, two small populations would experience significant losses of 92% and 95% due to rising lake levels.

The life history and ecology of Shasta snow-wreath is not well studied. To date, little work has been conducted on the basic demography of Shasta snow-wreath or its response to common disturbances such as fire and herbivory. We are aware of one study by Sierra Pacific Industries in which the response of a portion of a single Shasta snow-wreath population to timber harvesting is being monitored, though these results are not yet published (T. Engstrom, Sierra Pacific Industries personal communication).

Shasta snow-wreath is deciduous and bears flowers with showy stamens and 0–2 petals at the base (Fig. 2). Fruits are rarely observed and the species is thought to reproduce primarily vegetatively, forming thickets of stems arising from the root system (Stebbins 1993). One study (DeWoody et al. 2012) used isozyme analysis to assess genetic diversity within and among 23 Shasta snow-wreath populations and found that within-population variation was low, while among-population variation was high. Five of the populations sampled were composed of single genets and the average number of genets per population was 3.14. This supports the hypothesis that sexual reproduction is less common in Shasta snow-wreath than clonal propagation, and that gene flow among populations is quite low (DeWoody et al. 2012). Whether this evident isolation of populations is a result of recent changes due to the construction of Shasta Dam, increased geographic restriction over long periods of time, or due to another unidentified source of ecological or evolutionary pressure, is unknown. Regardless of the cause, the low number of populations, small popu-

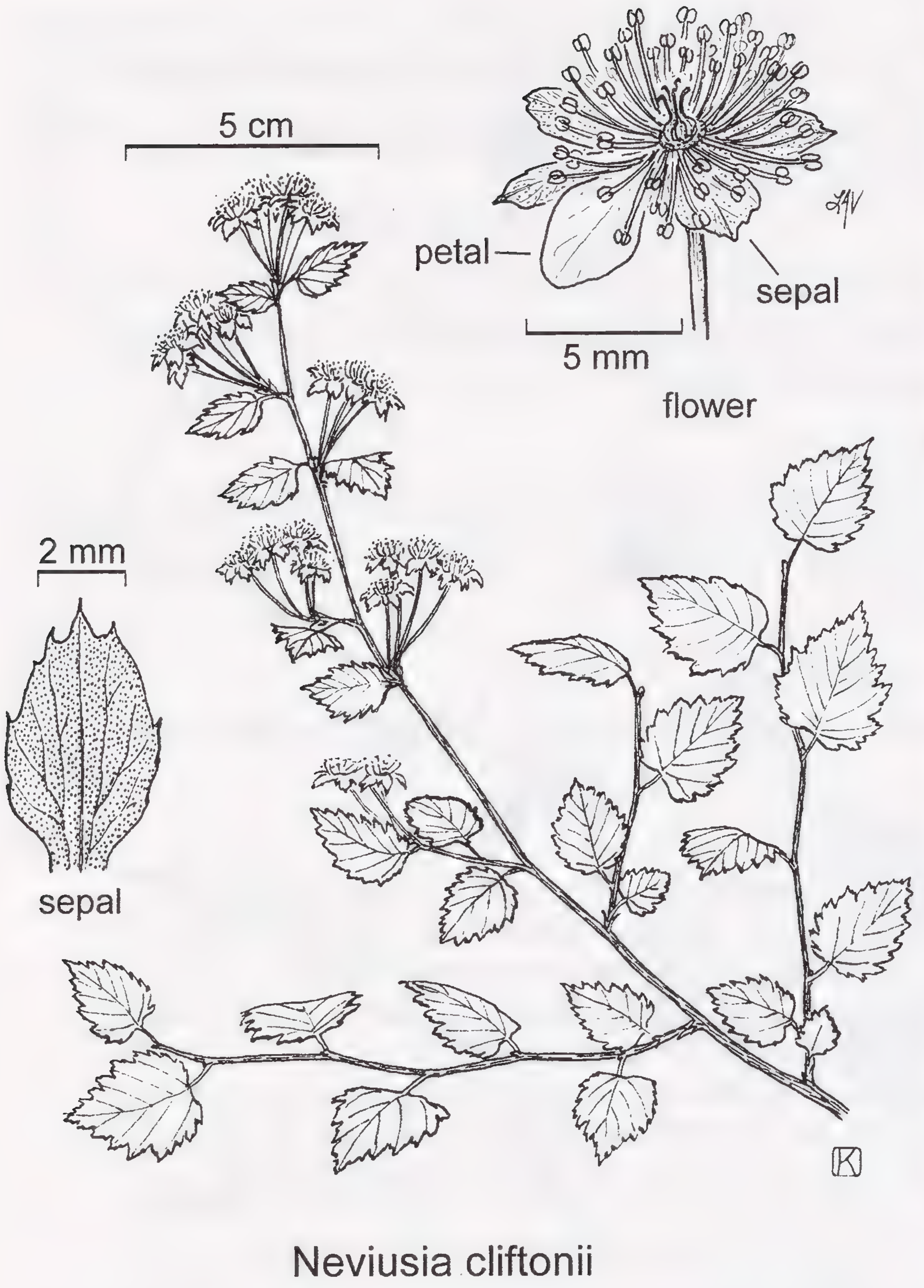

FIG. 2. Shasta snow-wreath (*Neviusia cliftonii* Shevock, Ertter & D.W. Taylor) illustration showing vegetative and reproductive structures. This rare shrub grows to a height of 2.5 m and is known from 33 populations near Shasta Lake, CA. Reprinted with permission from Baldwin et al. (2012).

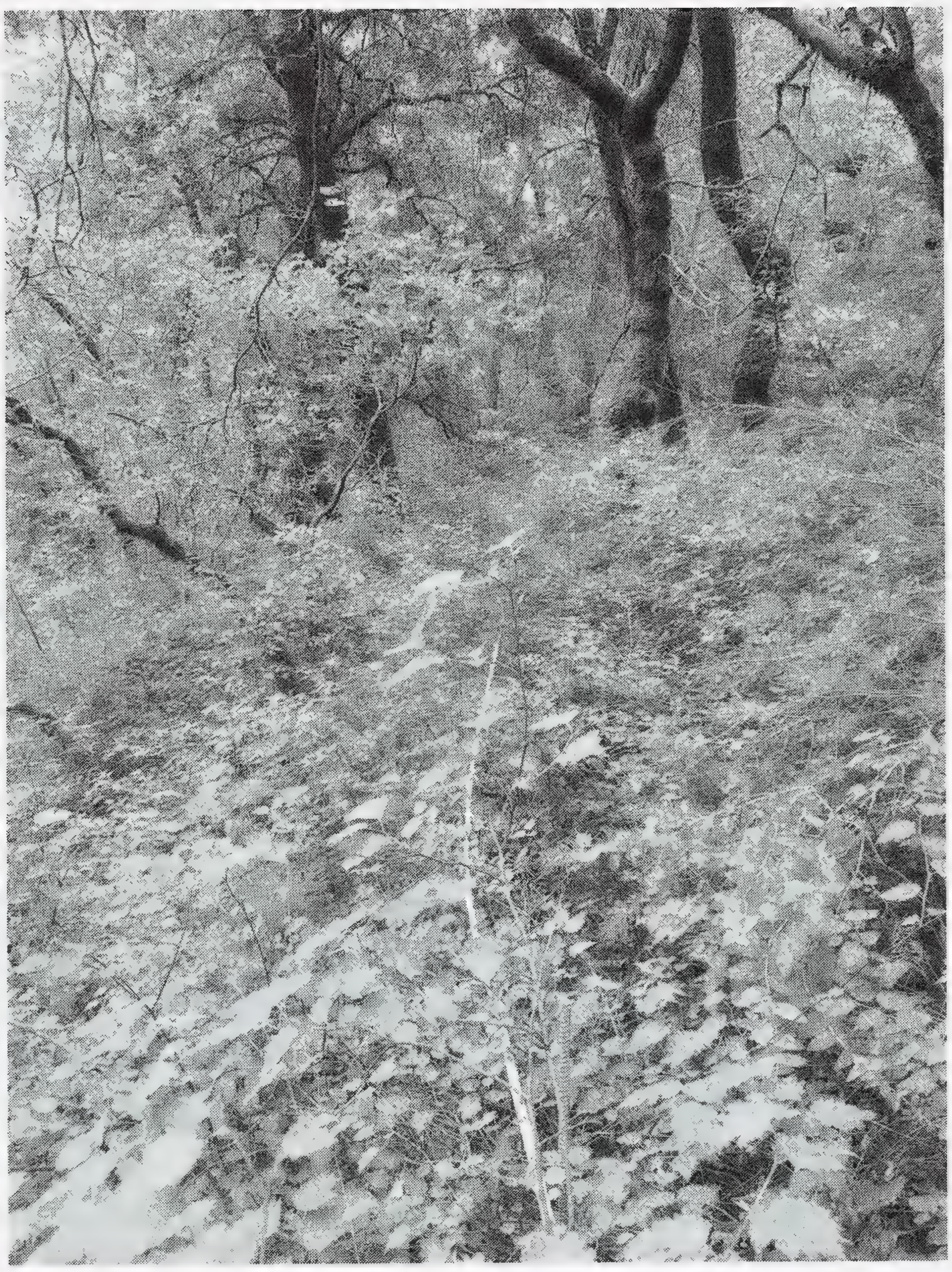

FIG. 3. Typical habitat of Shasta snow-wreath (*Neviusia cliftonii* Shevock, Ertter & D.W. Taylor) with a permanently-marked transect at the Waters Gulch site (Table 1). The dominant canopy trees shown here are canyon live oak (*Quercus chrysolepis* Liebm.). Photo courtesy H. Kurkjian.

lation sizes, and low within-population diversity all suggest that careful monitoring of the species is warranted (Ellstrand III and Elam 1993; Schemske et al. 1994).

The primary goal of our work was to describe population characteristics of Shasta snow-wreath, including size, density, associated vegetation, and abiotic site characteristics. Additionally, we used our data to explore the relationships between population metrics (e.g., number of stems, or ramets, per population) with site characteristics to better understand what factors might influence Shasta snow-wreath. To do this, we established permanent plots within eight of the 33 known populations. While the number of plots is relatively small, the study included detailed observations at each site. Additionally, the system of plots was created to allow for long-term monitoring efforts and for an expansion of the methodology to other populations. In particular, these plots will be used to assess population trends over time with special attention to understanding the impact of fire. In the study area, fire is particularly important as increases in temperature and climate water deficits have increased the likelihood for greater extent and frequency of fires in the region (Miller et al. 2009).

METHODS

Data Collection

During the summers of 2011–2013, we established eight permanent transects for population surveys and future monitoring of Shasta snow-wreath (Table 1; Fig. 3). Specific sites were chosen by finding relatively large patches of Shasta snow-wreath (at least ~40 m^2) through which we could establish a 2-m wide belt transect. Sites were selected such that they were distributed among the known populations and easily accessed along roads or by boat. Several populations were excluded because they were located on private lands or were very small (J. Nelson, U.S. Forest Service, L. Lindstrand III, North State Resources, Inc., personal communication). We positioned transects through the center of each population, recorded their length and bearing, and installed metal stakes (rebar) at both ends. We recorded plot elevation and UTM coordinates using a Trimble Nomad or Juno 3B GPS unit (Trimble, Sunnyvale, CA, USA). We also recorded topographical characteristics of each site, including the shape, position, aspect, and degree of slope.

TABLE 1. Topographical characteristics recorded at eight Shasta snow-wreath populations. Population names ("Site") correspond to those found in DeWoody et al. 2012 (with the exception that our study used Waters Gulch twice). "CNDDB element #" lists the California Natural Diversity Database (CNDDB) element occurrence number. "Order 3 soil type" is from USDA Forest Service (1983) and "Geologic soil type" is from USDA Forest Service (2004).

Site	CNDDB element #	Elev. (m)	Aspect	Slope (°)	Slope position	Order 3 soil type	Geologic soil type
Blue Ridge	16	332	22	35	Backslope	Holland	Shale; siltstone; metavolcanic; w/ limestone; & undiff.
Campbell Creek	6	336	22	21	Toeslope	Holland/Goulding	Tuffaceous mudstone w/lesser mafic flows; sandstone; cherty quartzite; other ms; & undiff.
Curl Creek	5	397	16	35	Backslope	Holland	Greenstone & greenstone breccia
Jones Valley	21	323	20	35	Footslope	Marpa Holland	Shale; siltstone; metavolcanic; w/ limestone; & undiff.
Low Pass	7	473	240	10	Shoulder	Marpa-Neuns	Limestone; thin-bedded to massive; gray; fossiliferous
Stein Creek	12	332	55	65	Backslope	Neuns	Andesitic volcaniclastic & pyroclastic rocks; conglomerate; & undiff.
Waters Gulch	14	311	18	28	Backslope	Holland	Greenstone; & undiff.
Waters Gulch 2	14	425	323	65	Shoulder	Holland	Greenstone; & undiff.

Of the eight total plots, we established seven in 2011 and added one additional site (Waters Gulch 2) in 2012 (Table 1). Although we had anticipated sampling all eight populations in 2012 and 2013, low water levels in Shasta Lake made accessing some of the sites difficult because they are most easily reached by boat. Thus, we were unable to sample Campbell Creek in 2012 and Stein Creek in 2013. The U.S. Forest Service performed a small prescribed burn in December 2011 which partially burned the Jones Valley population, including 50% of our transect. We were unable to assess the precise response of Shasta snow-wreath to the fire because soil slumping near the base of the slope shifted the rebar used to mark the exact start location of our transect at that site. However, we did flag burned patches immediately post-fire and we report on our qualitative observations of fire effects from the site in 2012 and 2013.

In each population we characterized Shasta snow-wreath by sampling in 1 m quadrats along both sides of the entire transect, forming a belt transect that was 2 m wide. In each quadrat, we recorded the number of Shasta snow-wreath stems, the number of inflorescences per stem, and the height of the tallest stem. We also recorded the width of the population at the initial transect origin, at each 5 m increment along the transect, and at the transect endpoint. These measures were used to determine the total area of the population. We also characterized other species associated with Shasta snow-wreath populations by recording the rank order of dominant trees and, separately, shrubs found within the population area. We also sampled each belt transect for ground and vegetative cover. Ground cover measurements included the percent cover bare ground (particles < 2 mm), gravel (particles 2–15 mm), rock (particles > 15 mm), woody debris (stems > 7.62 cm diameter), litter (stems < 7.62 cm diameter), and total basal vegetation (all live plants combined). Vegetative cover measurements included the percent cover of live and dead trees, live and dead shrubs, forbs, ferns, moss, grass, and lichen. We also recorded the percent cover of all invasive plant species (defined by Cal-IPC 2006) in the belt transect and noted any invasive species present in the remainder of the population. Lastly, we extended a separate Brown's Fuels transect (Brown 1974) in a randomly selected direction from the belt transect origin at each site and recorded the number of 1-, 10-, 100-, and 1000-hr fuels. At each 5 m length of the fuels transects we recorded litter and duff depth.

Analyses

For each site, we averaged all observations across all years that were sampled. We did this for two reasons: (1) we did not have a record of all sites in all years and, (2) site- and population-level data did not vary considerably from year to year. We then summarized each plot's topography, vegetation, and Shasta show-wreath population characteristics. We calculated the mean Shasta snow-wreath stem density, number of inflorescences per stem, and average maximum height. We then estimated the total number of stems in each population by scaling the density of stems within the belt transect to the total population area. Because multiple stems may belong to a single genet, we consider our stem counts to be ramet counts. That is, rather than estimating "population sizes" per se, we estimated "ramet population sizes" and use that terminology throughout. Individual sites were averaged across years for vegetation and ground cover metrics as well as fuel loads (see Tables 2 and 3). We transformed aspect to linear aspect using the equation

$$lASP(i) = 1 + cos\frac{\pi(aspect(i) - 45)}{180}.$$

where $lASP(i)$, and $aspect_i$, are the linear aspect and aspect of the site i, respectively. The transformation

TABLE 2. Summary statistics for eight Shasta snow-wreath populations. All values are averages across all years for which observations were made in belt transects, except for two categories: "Population area" is the estimated total geographic area of the population, and "Ramet population size" is the number of stems in the estimated population area. See Methods section for details.

Site	Years surveyed	Transect length (m)	Population area (m^2)	Number of inflorescences	Average number of inflorescences per stem	Average maximum height (m)	Number of stems counted	Ramet population size
Blue Ridge East	3	20	365.5	569	0.98	115	566	4585
Campbell Creek	2	25	232.9	733	3.34	92	209	1022
Curl Creek	3	29	310.3	329	1.02	69	317	1729
Jones Valley	3	20	410.8	30	0.08	50	359	3878
Low Pass	3	25	1366.7	3391	7.92	142	417	11,708
Stein Creek	2	20	129.4	1089	4.91	73	215	716
Waters Gulch	3	9	86.3	230	0.75	129	292	1459
Waters Gulch 2	2	25	1007.6	2830	3.06	159	847	18,641

results in values that range from 0.0 (warmer, drier southwest-facing slope) to 2.0 (cooler, moister northeast-facing slopes). To determine if any of the demographic characteristics of Shasta snow-wreath populations are associated with site characteristics, we used Spearman's rank correlations. Specifically, we assessed correlations between topographical, vegetation and ground cover characteristics and the estimated Shasta snow-wreath ramet population size, average maximum height (cm), and number of inflorescences per stem. In addition, we described the dominant vegetation associated with Shasta snow-wreath by summing the ranking of dominant trees and shrubs associated with each site across all years.

RESULTS

The eight Shasta snow-wreath populations we studied occur from 332 m to 473 m elevation and on slopes of varying steepness (10° to 65°, Table 1). Most populations occur on north-facing slopes and on the backslope positions (Table 1). The permanently marked transects established in each population ranged from 9 m to 29 m (mean = 21.6 m). The number of stems observed in these transects varied from 160 to 932, and, when averaged across the years sampled for each population, varied from 220 to 925 (Table 2). The geographical area of populations varied from 86 m^2 to 1367 m^2 (mean = 489 m^2, Table 2). The average Shasta snow-wreath population we sampled consisted of an estimated 5467 stems (range = 716 to 18,641, Table 2). Populations also differed with respect to the number of inflorescences; the number of inflorescences ranged from 0 to 4231, and averages across years for each site ranged from 30 to 3391 (Table 2). The average maximum height of Shasta snow-wreath was 104 cm and ranged from 50 to 159 cm (Table 2).

All sites were characterized by relatively high cover of live shrubs (51% to 96%) and live trees (68% to 95%). The percent cover of other vegetation (forbs, ferns, grass, and lichen) was relatively low among all sites (<10%; Table 3), although, the cover of moss varied between sites with the greatest cover observed at Campbell Creek (31%) and Stein Creek (87.5%; Table 3). The study sites included very low cover of dead shrubs (0.25% to 1.25%) and dead trees (0.25% to 1.33%; Table 3). At most sites the ground was mostly comprised of litter (41.5% to 97.66%) and in some cases moss (see Campbell Creek and Stein Creek). We observed low cover of bare ground (0.25% to 2.83%), rock (0.16% to 1.75%), woody debris (1% to 7.33%) and basal vegetation (1% to 2.33%). We observed the invasive plant Himalayan blackberry (*Rubus armeniacus* Focke) in three of the eight sites (Blue Ridge, Low Pass, and Campbell Creek) where its cover reached as

TABLE 3. Average percent vegetative cover recorded at each site across all survey years (2011–2013). Vegetation cover metrics included the percent ground cover and percent vegetation cover on other species (e.g., the percent cover moss category includes cover on the ground and other organisms).

Site	Live Tree	Dead Tree	Live shrub	Dead shrub	Forb	Fern	Moss	Grass	Lichen	Bare ground	Rock	Woody Debris	Basal Veg.	Litter
Blue Ridge East	75	0.66	97	1.25	0.75	0.5	7.75	0.5	0.25	1	0.5	2	1.5	92.66
Campbell Creek	95	0.5	94	0.25	1.25	1.25	31	2.25	0.5	0.5	0.75	3.5	2	59
Curl Creek	88	0.33	91.33	1	1.5	2.16	3.83	0.16	0.33	0.5	0.5	2.66	1.5	94.16
Jones Valley	88.3	1.33	51.66	0.5	0.66	1	1	0.16	0.16	2.83	0.5	1	1.33	95
Low Pass	68.3	1.33	96.33	0.5	2.16	0.16	2.66	0.5	0.5	0.5	0.16	7.33	2.33	88
Stein Creek	90	0.25	85	4	5.25	7.5	87.5	0.5	0.5	1	0.5	5	2	41.5
Water's Gulch	86.7	0.5	88	0.5	1.66	0.33	0.5	0.66	0.16	0.16	0.33	1.33	1	97.66
Water's Gulch 2	77.5	0.25	94.5	1	0.5	0.25	1	0.25	0.5	0.25	1.75	1.25	1.25	95.5

TABLE 4. Ranking of the 15 dominant tree and shrub species associated with eight Shasta snow-wreath populations across all sites and all years. Species were ranked at each site (e.g., 1, 2, 3, etc…) and those species with the lowest sum across sites are ranked as most abundant. See text for details.

Rank	Dominant Trees	Dominant Shrubs
1	*Quercus kelloggii* Newb.	*Neviusia cliftonii* Shevock, Ertter & D.W. Taylor
2	*Pseudotsuga menziesii* (Mirb.) Franco	*Toxicodendron diversilobum* (Torr. & A. Gray) Greene
3	*Acer macrophyllum* Pursh	*Rosa* spp.
4	*Quercus chrysolepis* Liebm.	*Styrax redivivus* (*Torr.*) L.C. Wheeler
5	*Pinus ponderosa* P. Lawson & C. Lawson	*Aralia californica* S. Watson
6	*Quercus wislizeni* A. DC.	*Philadelphus lewisii* Pursh
7	*Umbellularia californica* (Hook. & Arn.) Nutt.	*Symphoricarpos albus* (L.) S.F. Blake
8	*Quercus garryana* Douglas ex. Hook.	*Rubus* spp.
9	*Cornus* spp.	*Cornus* spp.
10	*Aesculus californica* (Spach) Nutt.	*Staphylea bolanderi* A. Gray
11	*Pinus sabiniana* Douglas ex. G. Don	*Berberis* spp.
12	*Alnus rhombifolia* Nutt.	*Ribes* spp.
13	*Fraxinus latifolia* Benth.	*Corylus cornuta* Marshall
14	*Pinus attenuata* Lemmon	*Frangula californica* (Eschsch.) A. Gray
15	*Salix* spp.	*Calycanthus occidentalis* Hook. & Arn.

high as 7.5% (Low Pass). Six of our eight populations were found on north-northeast facing to northwest-facing aspects (between 16° and 55°), while Low Pass and Waters Gulch 2 were found on northwest-facing and southwest-facing aspects, respectively (Table 5). We found that the eight Shasta snow-wreath study populations had, on average, 81,337 kg ha^{-1} dry biomass and most of this fuel (~60%) was comprised of fine fuels (<7.6 cm diameter; 1-, 10-, 100-hr fuels). Fine fuels, which are associated with wildfire risk, ranged from 5422 kg ha^{-1} to 134,064 kg ha^{-1} among our populations (mean = 48,624 kg ha^{-1}).

We recorded 17 tree and 36 shrub species that were associated with Shasta snow-wreath (Table 4). The most common tree species we recorded were California black oak (*Quercus kelloggii* Newb.), Douglas-fir (*Pseudotsuga menziesii* Mirb.), big-leaf maple (*Acer macrophyllum* Pursh), and canyon live oak (*Quercus chrysolepis* Liebm.), while the most common shrubs were the Shasta snow-wreath, poison oak (*Toxicodendron diversilobum* [Torr. & A. Gray] Greene), roses (*Rosa* spp.), and snowdrop bush (*Styrax redivivus* [Torr.] L.C. Wheeler; Table 4).

TABLE 5. Spearman's non-parametric correlations between site cover characteristics and individual and population-level Shasta snow-wreath characteristics including the average number of inflorescences per stem, average maximum height (m), and estimated ramet population size. ** denotes significant associations ($\alpha = 0.05$) and * denotes marginally significant associations ($0.05 < \alpha < 0.1$).

	Inflorescences per stem		Average maximum height (m)		Ramet population size	
	r_s	P	r_s	P	r_s	P
Slope	−0.21	0.772	−0.04	0.918	0.21	0.611
Aspect	−0.76	0.028**	−0.63	0.094*	−0.71	0.045**
Elevation	0.66	0.075*	0.52	0.183	0.74	0.036**
Fern	−0.2	0.615	−0.51	0.196	−0.44	0.278
Forb	0. 5	0.212	−0.25	0.893	−0.54	0.389
Grass	0.17	0.683	−0.01	0.996	−0.32	0.435
Live Tree	−0.42	0.292	−0.69	0.058*	−0.72	0.050**
Dead Tree	0.16	0.7	−0.09	0.862	0.11	0.791
Lichen	0.82	0.014**	0.3	0.468	0.39	0.336

A low-intensity prescribed burn at the Jones Valley site in December 2011 burned approximately 50% of the transect. We observed basal resprouting (Fig. 4) and evidence of deer browse throughout the burned portion of the population during resampling in summer 2012. In small patches where the shrubs appear to have been top-killed by the burn, resprouting was still evident. Herbivory was limited to the new growth.

The eight Shasta snow-wreath populations that we studied varied considerably in both vegetative and reproductive characteristics. Some of this variation, but not all, could be explained by site characteristics we measured. We found a significant correlation between aspect and the estimated number of inflorescences per stem ($r_s = 0.76$, $p = 0.028$, Table 5); the least number of inflorescences per stem was found in the four most north-facing sites (16–22°, Table 2). Additionally, we found a marginally significant increase in the number of inflorescences at higher elevations ($r_s = 0.66$, $p = 0.075$) and a significant increase in sites with a higher percent cover of lichen ($r_s = 0.82$, $p < 0.014$; Table 5). We have no measure of precipitation at our study sites, although precipitation may increase in elevation and be a more proximal cause of more inflorescences. Average maximum height (cm) of Shasta snow-wreath was greatest in sites with the smallest percent cover of live trees, though this relationship was marginally significant ($r_s = -0.69$, $p = 0.058$). Also, the relationship of average maximum height and aspect was marginally significant ($r_s = -0.63$, $p = 0.094$); the same sites that had high inflorescence density had tall stems (Table 2). The estimated ramet population sizes were significantly larger in sites at higher elevations ($r_s = 0.74$, $p = 0.036$) and with lower

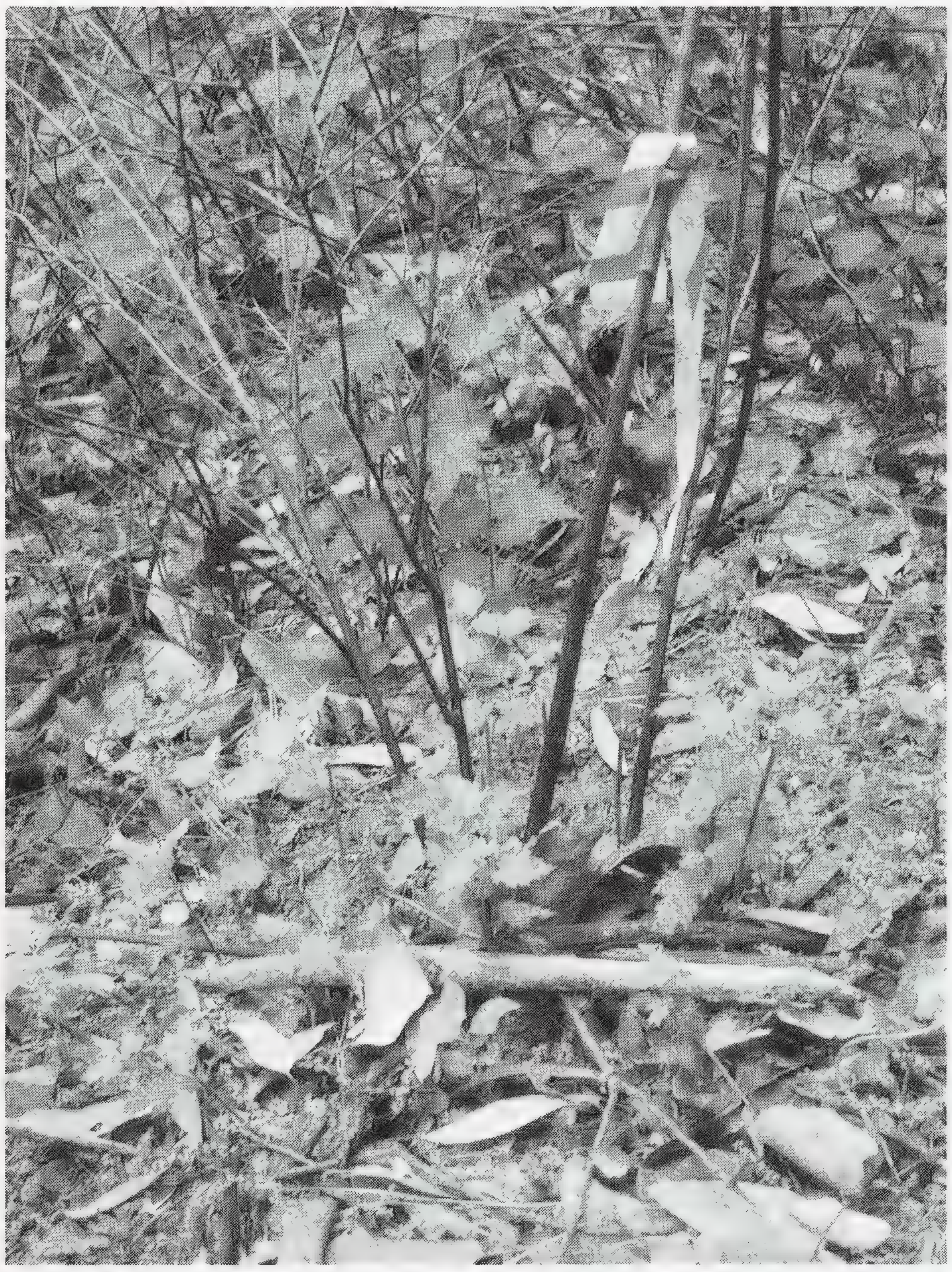

FIG. 4. Evidence of resprouting on Shasta snow-wreath (*Neviusia cliftonii* Shevock, Ertter & D.W. Taylor), seven months after a 2011 prescribed burn at the Jones Valley site (Table 1). The dominant canopy trees shown here are canyon live oak (*Quercus chrysolepis* Liebm.). Photo courtesy R. Butz.

cover of live trees ($r_s = -0.71, p = 0.05$). Likewise, the most north-facing sites had the smallest estimated number of ramets ($r_s = -0.72, p = 0.045$; Table 5). We note that when evaluating these correlations, we have not adjusted the level of significance (α) to reduce the risk of Type I errors when using multiple comparisons. For instance, a Bonferroni adjustment would result in $\alpha = 0.0019$ ($0.05 \div 27$ tests). Instead, we present unadjusted *P*-values as a means of exploring potential hypotheses about Shasta snow wreath distribution and limit our conclusions based on the relatively small size of the study.

DISCUSSION

Overall, the population structural information we collected suggests some interesting hypotheses about the factors that control Shasta snow-wreath populations. Our largest ramet population sizes, and our tallest individuals, were found in sites with relatively low canopy cover of live trees (Tables 2 and 5). This relationship is intriguing and suggests that removal of the canopy by fire may have been a critical disturbance for this rare shrub. The California black oak woodlands and Pacific ponderosa pine – Douglas-fir forests (Eyre 1980) where Shasta snow-wreath populations occur exhibit very high departures from pre Euro-American settlement fire frequencies (Safford and Van de Water 2014) and the presence of relatively fire-intolerant Douglas-fir in the overstory is indicative of prolonged fire suppression. Historically, this vegetation experienced frequent wildfires with an average fire return interval of 12 years (Taylor and Skinner 2003; Fry and Stephens 2006; Safford and Van de Water 2014). Restoring a more frequent fire return interval through prescribed burning or employing a mechanical fuels treatment to reduce canopy cover may benefit Shasta snow-wreath. However, we do not know how Shasta snow-wreath would respond to higher severity wildfire under these fire-suppressed conditions where fuel loads may be elevated. Our measures of current fuel loads should be useful for long-term monitoring.

Lastly, the two largest populations (Low Pass and Waters Gulch 2) were notable in that they were at relatively high elevations and their aspects were westerly-facing, while the other six populations were all found in a small range of aspects (16° to 55°; Table 1). These same populations tended to have more inflorescences per stem as compared with other populations. However, the relationship of aspect and population characteristics is confounded by a positive relationship between live canopy and aspect ($r_s = 0.78, p = 0.022$; Table 5). Thus, expansion of our monitoring program to include more of the other 33 populations—across a broad range of aspects—would help elucidate the roles of canopy, aspect, and other site characteristics. Also, several additions should be made to the monitoring program. Himalayan blackberry occurred in three of our eight sites and was common in the general study area, so assessing its impact on Shasta snow-wreath across a larger number of populations is warranted. Finally, little is known about the potential impacts of herbivores, pathogens and pollinators on Shasta snow-wreath and these are worth pursuing in future work. Overall, this monitoring effort has provided a baseline from which to pursue repeat measure of existing permanent plots and a basis for expansion of studying other Shasta snow-wreath population characteristics.

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